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Dispersal Limitation and Climate-Related Environmental Gradients Structure Microcrustacean Composition in Freshwater Lakes, Ellesmere Island, Canada

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Dispersal limitation and climate-related environmental gradients structure microcrustacean composition in freshwater lakes, Ellesmere Island, Canada

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Abstract

Dramatic environmental change is expected in the Arctic, yet little is known about the occurrence and community composition of microcrustaceans in Arctic lakes and how the distribution of these freshwater organisms will be influenced by future environmental change. To further this understanding, microcrustaceans were sampled in 54 lakes on Ellesmere Island, Canada, and species relative abundances were calculated for each lake. New records of species found on Ellesmere Island included *Daphnia umbra, Tachidius discipes* and *Artemeopsis stefanssoni. Daphnia middendorffiana/tenebrosa* was the most commonly found taxon and often dominated microcrustacean assemblages, likely a result of the competitive advantage it derives from pigmentation, which offers UV resistance. Species richness was positively associated with nutrients, DOC, temperature, calcium, and conductivity, and negatively affected by elevation. In contrast to most findings in temperate systems, we detected a negative relationship between species richness and surface area. Microcrustacean community composition was influenced by DOC, nutrients, and elevation, but also exhibited strong relationships with spatial variables, suggesting that spatial gradients in environmental conditions and dispersal are important drivers of differences among sites. Species with effective dispersal mechanisms, such as *Daphnia middendorffiana/tenebrosa*, tended to be distributed at broad spatial scales. Arctic ecosystems are expected to change rapidly in the coming years due to climate change and ozone thinning, and we expect associated changes in DOC, temperature, and nutrients will impact microcrustacean species richness, distribution, and dispersal throughout the landscape.

Introduction

Relatively little information exists about the aquatic communities of the many hundreds of lakes throughout the High Arctic, with the exception of ongoing research on freshwater diatom assemblages (Douglas et al. 2004). Yet with increasing climate change, the Arctic is expected to be one of the most severely affected areas (ACIA 2005). Evidence based on paleolimnological studies suggests that biological communities in lakes and ponds in High Arctic regions have already experienced dramatic and unprecedented shifts in composition during the past 150 years, most likely associated with longer ice-free seasons and associated changes in lake productivity (Smol et al. 2005). In addition, recent research has revealed that chemical pollutants, including mercury and brominated flame retardants, are ubiquitous in Arctic lakes and biota (de Wit et al. 2006; Evans et al. 2006). To further our understanding of how these and other stressors will influence the structure and functioning of aquatic ecosystems, it is first necessary to determine what factors control the spatial distribution and local structure of Arctic aquatic food webs.

Microcrustaceans play a pivotal role in aquatic systems, transferring energy from primary producers to higher trophic levels. They likely have even greater ecological significance in the High Arctic, where food webs are simplified and the majority of lakes are fishless, owing to their shallow depth (Hershey et al. 2006). In addition, microcrustaceans are sensitive indicators of environmental conditions, as many species have short generation times and widely varying environmental preferences and tolerances. However, little is known about the species composition and distribution of microcrustaceans on Ellesmere Island in the Canadian High Arctic. The studies that have been done in this area have been mostly restricted to the Lake Hazen area. McLaren (1964) sampled microcrustaceans from Lake Hazen, as well as a nearby

pond, finding a total of 8 microcrustacean species. A more wide ranging survey (~38 km^2) was conducted by Røen (1981); however, this too was restricted to the Lake Hazen area, although 60 lakes were sampled and 22 species were collected. A more recent study of one lake and a fjord outside of the Lake Hazen basin found only two calanoid copepod species (Van Hove et al. 2001).

Microcrustaceans in temperate regions have been well-studied and a number of factors have been linked to their species richness and composition. These include primary productivity (Dodson 1992; Dodson et al. 2000), nutrient concentrations (Jeppesen et al. 2000; Sweetman and Smol 2006b), lake size (Dodson 1992), pH (Pinel-Alloul et al. 1990; Walseng et al. 2003), calcium, sulphate, and magnesium (Pinel-Alloul et al. 1995), total dissolved solids (Chengalath 1982), and predation (Keller and Conlon 1994). In addition, spatial factors relating to the distribution of lakes across the landscape may also affect microcrustacean community composition by influencing the dispersal of individuals between neighboring sites. Pinel-Alloul et al. (1995) divided variation into that explained by purely environmental variables (e.g., water chemistry), purely spatial variables (e.g., a latitudinal gradient) and spatially-structured environmental variables (e.g., an environmental gradient across the study area), and found that although microcrustacean community composition depended on both environmental and spatial factors, purely spatial variables did not significantly increase the amount of variation that could be explained. However, Cottenie et al. (2003) detected a significant contribution of purely spatial variation in microcrustacean community composition, but found that spatially-structured environmental variation was minor, likely because their study area was small (2 km^2) compared to that of Pinel-Alloul et al. (1995) (3×10^5 km^2), and thus did not possess a strong environmental gradient. In addition, Beisner et al. (2006) found that space was a significant driver of

87 microcrustacean community composition when both overland and watercourse distance were
88 considered, suggesting that microcrustaceans may disperse equally well via water and aerial
89 connections.

90 Although there have been relatively few studies compared to temperate regions, several
91 studies of patterns in microcrustacean community structure have been conducted in the Arctic.
92 Hebert and Hann (1986) surveyed microcrustacean communities across the North American
93 Arctic, from Churchill, Manitoba (58°47′N) to Polar Bear Pass, Nunavut (75°42′N) and from
94 Cape Thompson, Alaska (165°46′W) to Frobisher Bay, Nunavut (68°30′W). They found 9-16
95 microcrustacean species in ponds in glaciated regions of the lower Arctic and 4-10 species in
96 sites on islands in the Canadian High Arctic archipelago (Hebert and Hann 1986). A study of
97 similar scope in the Yukon and western Northwest Territories found a total of 19 crustacean
98 species, where abiotic variables (chloride, silica, and temperature) explained 25% of the
99 variation in species composition (Swadling et al. 2000). A survey of 104 Alaskan Arctic lakes
100 revealed that lake surface area and depth were important drivers of microcrustacean richness,
101 while water chemistry and fish composition were insignificant (O'Brien et al. 2004). The Arctic
102 undergoes periods of severe ozone depletion (Bottenheim et al. 2002). This is expected to worsen
103 as atmospheric carbon dioxide levels rise (Austin et al. 1992), cooling the stratosphere, and
104 activating ozone-depleting compounds, suggesting that UV radiation may play an important role
105 in high latitude locales. However, studies in the Arctic have failed to ascertain whether UV and
106 UV-related factors (e.g., dissolved organic carbon (DOC)) influence microcrustacean community
107 structure. In addition, none of these studies considered spatial variables as predictors in their
108 analyses. Given the high number of lakes and ponds in Arctic regions, we expect that spatial
109 variables (and therefore dispersal) will be important determinants of microcrustacean community

structure.

For this study, we had three objectives: 1) to document microcrustacean species found in the northern third of Ellesmere Island, 2) to determine what potential drivers are associated with species richness and community composition, and 3) to investigate the relative importance of spatial versus environmental variables in determining species composition using powerful, newly developed statistical techniques, generally referred to as distance-based eigenvector maps (Borcard and Legendre 2002; Dray et al. 2006; Griffith and Peres-Neto 2006). In the past, spatial variables have been incorporated in ecological studies using polynomials of geographic coordinates (trend surfaces) (Borcard et al. 1992). However, this approach is not well-suited to sampling in heterogeneous areas or irregular sampling designs, and can only generate broad-scale spatial structures (Dray et al. 2006 and references therein). The advantage of distance-based eigenvector map techniques is that they offer flexibility in sampling design and are able to generate structures at a range of spatial scales (Borcard and Legendre 2002), allowing for the description of biological phenomena, such as seed dispersal, that may occur very locally or very broadly. Thus far, there has been little research aimed at understanding the controls on species richness and composition in the Canadian High Arctic, and how they may differ from the trends found in temperate zones.

Materials and Methods

Study Site and Sampling

Ellesmere Island (Fig. 1) is the most northern landmass in Canada and is located in the High Arctic. Ellesmere is a region of continuous permafrost, where the winters are long and cold and the summer growing season lasts only 8 to 12 weeks (Lévesque et al. 1997). Several glaciers

remain, dominating the landscape, affecting the surface materials and the climate of Ellesmere Island. Lake Hazen is a large lake north of 80º N latitude and the area surrounding it is generally warmer and has more lush vegetation cover than other areas of Ellesmere Island (Keatley et al. 2007), due to protection from cold air flows by the surrounding mountain ranges.

Fifty-four lakes or ponds were sampled throughout the northern third of Ellesmere Island; waterbodies were named arbitrarily by the order in which they were sampled, and official lake names, locations, and morphometry are listed in Supplementary Table S1. Samples were taken from 24 lakes in the Lake Hazen basin (81˚49′N to 81˚51′N), the lowlands immediately surrounding Lake Hazen. The remaining 30 samples were taken from lakes distributed over the northern third of Ellesmere Island (80˚36′N to 83˚05′N), primarily in the Grant Land Mountains region. A number of sites were located in coastal areas, and elevated calcium and conductivity values in these lakes likely indicate a marine influence (Supplementary Table S1). However, the highest calcium and conductivity concentrations were observed in inland lakes around the polar oasis Lake Hazen, which may be due to the influence of the local bedrock in some sites, but in others likely reflects increased evaporation due to warming, resulting in increased concentrations of solutes (Keatley et al. 2007).

Water samples for chemical and chlorophyll *a* analyses were taken by submerging a 1-L Nalgene® bottle below the water surface. Surface water temperature was measured near the shore using a handheld mercury thermometer. Conductivity and pH were measured using a portable Hanna® pHep 3 meter (Woonsocket, Rhode Island) and a YSI 33 conductivity meter (Yellow Springs, Ohio), respectively. Water samples were sent to Environment Canada's National Laboratory for Environmental Testing for analysis of major ions, nutrients, and metal concentrations (Environment Canada 1994) (Table 1, Supplementary Table S1). A known

volume of water was filtered through Whatman® GF/C filters (pore size: 1.2 μm), which were then frozen in snow and kept in darkness for chlorophyll *a* analysis at Environment Canada (1994). Where sites were reached by helicopter, elevation was determined by altimeter. In other cases, it was estimated from National Topographic System maps. Length and width of each lake or pond were obtained from measurements using a laser distance finder, or from the National Topographic System maps. Lake surface area was estimated from width and length measurements using the formula for an ellipse. We were not able to access lakes by boat, and because of limited information about lakes in this area, mean and maximum lake depths are not available.

Microcrustaceans were collected between 6 July and 18 July 2003 using a 15-cm diameter, 80-μm mesh net, fastened to the end of a fishing rod. Several qualitative horizontal tows were taken from the surface waters within wading distance from the shore, as the ponds were too shallow to sample quantitatively. All lakes and ponds were sampled for approximately the same amount of time (i.e., similar sampling effort) and microcrustaceans were preserved in a ~4% formalin solution. In a comprehensive study of >2400 lakes in Norway, Walseng et al. (2006) found that there was a high degree of concordance in crustacean species identity in samples taken strictly from each of the littoral and pelagic zones, where all but 2 species that were found in pelagic samples were also found in littoral samples. Their study suggests that nearshore sampling can give an accurate assessment of microcrustacean assemblages in lakes, and thus, that our sampling effectively captured the diversity of microcrustacean taxa in lakes on Ellesmere Island. Additionally, both pelagic and littoral taxa are known to respond to environmental gradients (Walseng et al. 2003; Sweetman and Smol 2006b), and are therefore useful indicators of changing conditions in Arctic ecosystems.

Microcrustaceans were identified using a Leica MZ16 microscope (see Supplementary Table S2 for microcrustacean relative abundance in study sites), and were generally identified to species, with the exception of juvenile stages, ostracods, and members of the family Chydoridae, whose taxonomic affiliation at northern latitudes in North America is uncertain (Sweetman and Smol 2006a). Although Arctic *Daphnia* have genetic diversity that is comparable to that of temperate zone *Daphnia* (Hobæk and Weider 1999), genetic analysis was beyond the scope of this study, and thus, members of the Arctic *Daphnia pulex* group could not be identified as either *D. middendorffiana* or *D. tenebrosa*, as they showed similar morphological characteristics and are known to hybridize (Weider and Hobæk 2003). Henceforth, it will be referred to as *Daphnia middendorffiana/tenebrosa.* As well, *Bosmina freyi* and *Bosmina liederi* (DeMelo and Hebert 1994) are difficult to distinguish, and thus, will be referred to as *Bosmina freyi/liederi*. Two methods were used for counting the microcrustacean samples: samples with low abundances of microcrustaceans were counted in their entirety, while samples with greater abundances of microcrustaceans were halved multiple times using a Folsom plankton splitter, and fractions were counted in their entirety. The number of fractions counted was determined using species accumulation curves for each lake. Because sampling was not quantitative, microcrustacean relative abundances were calculated for each lake, both with juveniles included and excluded. Species richness, Shannon-Wiener diversity, and Simpson's measure of evenness ($E_{1/D}$) (Magurran 2004) were calculated from relative adult abundance. Higher values of both indices indicates greater diversity and evenness, and the maximum value of $E_{1/D}$ is 1.

Analyses

Multiple regression using the best subsets procedure in Statistica v.6 (StatSoft 2001) was

used to determine which environmental variables explained patterns in species richness. Many of the environmental variables were significantly correlated and thus, multicollinearity would have severely affected our results. Instead, we performed a principal components regression, which uses a principal components analysis (PCA) of environmental variables to generate linear combinations of variables, which are then used as explanatory variables in a multiple regression, removing the effects of multicollinearity (Graham 2003). By assessing the loadings of each environmental variable on the principal components axes, we were able to evaluate which variables were important predictors of species richness. Physical and chemical variables thought to be relevant to microcrustacean biology (i.e., calcium, TN, TP, DOC, conductivity, elevation, lake surface area, latitude, temperature) were selected for PCA and the first four principal components were chosen for multiple regression analysis. Dissolved metal concentrations were not considered in the analysis, as all were below the ranges found to be toxic in microcrustaceans (Baudouin and Scoppa 1974). Similarly, pH was excluded from analysis, as all lakes above the pH considered to be harmful to microcrustaceans ($pH < 6.0$, Marmorek and Korman 1993). Adjusted R^2, Mallows C_p, and Akaike's information criterion (AIC) were used to evaluate the strength of the regression models.

Multivariate ordination techniques were used to assess patterns of species abundances using CANOCO v. 4.5 (ter Braak and Šmilauer 2002). Similar to our multiple regression analyses, a reduced set of environmental variables, thought to be relevant to microcrustaceans, were chosen. Spatial variables were created by converting Cartesian coordinates (x,y) to a grid using a Lambert conformal conic projection, as UTMs (universal transverse mercator) become distorted in polar regions. Distance-based eigenvector maps were used to transform spatial coordinates to interpret the scale of spatial variation (Borcard and Legendre 2002; Dray et al.

2006; Griffith and Peres-Neto 2006). The transformation of a simple grid into more complex spatial variables at both fine and broader scales allows greater resolution of spatial variability in a sampling area. The program spacemakeR was used to create the eigenvector maps (Dray 2006) using the statistical language R (R Development Core Team 2006). A pairwise Euclidean distance matrix (d_{ij}) was computed from the newly created Lambert projection coordinates of sampling sites and was transformed into a truncated connectivity matrix (**W**), defined by the threshold value t, where

$$(1) \qquad \mathbf{W} = (w_{ij}) = \begin{cases} 0 & \text{if } i = j \\ 0 & \text{if } d_{ij} > t \\ [1 - (d_{ij} \,/\, \max(d_{ij})] & \text{if } d_{ij} \leq t \end{cases}$$

Thus, sites that are closer together are given greater weight in the analysis. The value t was determined by testing the neighbourhood connectivity of our sites by performing a Delaunay triangulation, Gabriel graph, relative neighbourhood graph, and sphere of influence (Legendre and Legendre 1998). By testing different neighbourhood connectivity methods, we are able to ascertain at what scale processes, such as dispersal, are operating at, since different methods have differing levels of connectivity. For example, the Delaunay triangulation method had an average of 5 connections per site in the Lake Hazen area with a large number of long distance connections, while the relative neighbourhood method had an average of 2 connections per site, with more localized neighbourhoods and fewer long distance connections. Fewer, more localized connections might be more important to microcrustaceans, which can disperse via water connections, wind, and waterfowl, all of which may be more important vectors at small spatial scales.

The spatial variables derived from each connectivity matrix were tested with the species

248 abundances in an ordination and we chose the connectivity method whose variables explained
249 the greatest amount of variation, which was the relative neighbourhood method in all cases.
250 Following this, eigenvectors were computed from the matrix **W** and ones associated with small
251 eigenvalues represent local structures, while those associated with large eigenvalues represent
252 regional scales (Dray et al. 2006). As an example, some of the eigenvectors generated for the
253 Lake Hazen sites are shown in Fig. 2, where the eigenvector representing the very broadest
254 regional scale has two distinct clusters of sites (Fig. 2a), and each successive eigenvector has
255 progressively more localized clusters of sites, culminating in the most fine-scale local spatial
256 eigenvector (Fig. 2d). It is important to note that although the spatial variables generated have
257 both positive and negative values, this simply separates sites into different clusters, and thus,
258 does not represent positive or negative relationships.
259 We performed ordinations on a subset of sites (the Lake Hazen region) and on the entire
260 set of lakes from Ellesmere Island. This allowed us to examine the species compositions at small
261 scales (i.e., < 10 km), where local factors, such as dispersal, would be expected to be greater than
262 at larger scales, in contrast with larger scales (> 300 km), where environmental gradients may be
263 a more important driver of differences in species composition, and dispersal would be limiting.
264 Site EPI was excluded from ordinations, as there were no organisms recovered in the sampling.
265 All species and juvenile stages were included in our ordinations, as some of the lakes had only
266 juveniles present. In addition, we tested the association of species with differing spatial scales
267 following Brind'Amour et al. (2005), where we classified the spatial variables into very broad-,
268 broad-, meso-, and fine-scale based on groupings of their eigenvalues (e.g., Fig. 2). We will use
269 this classification scheme throughout, referring to different spatial variables by their scale and
270 number, e.g., **broad1** represents broad spatial scale variable 1. We chose only significant

271 eigenvectors for the spatial submodels, tested each spatial submodel in an RDA, and then used
272 the species loadings on the first canonical axis to interpret which species were most influenced
273 by different spatial scales.

274 A detrended correspondence analysis was conducted on species abundances to assess the
275 length of the environmental gradient, from which it was determined that redundancy analysis
276 (RDA) was appropriate. Species abundances were Hellinger-transformed to reduce the influence
277 of rare species (Legendre and Gallagher 2001). We tested if there was a linear spatial gradient in
278 species abundances, and it was removed from the whole Ellesmere Island set by taking the
279 residuals of the *x,y* coordinates and species abundances. Forward selection with 499 Monte-Carlo
280 permutations was used to determine which individual environmental and spatial factors had a
281 significant impact on the community composition. Collinearity was detected if the variance
282 inflation factor was >20 (ter Braak and Šmilauer 1998). Environmental variables that were not
283 significant were plotted as supplementary values, which act passively and have no influence on
284 the ordination diagram.

285 Variation partitioning techniques were used to determine the relative influences of purely
286 environmental (*en*), spatially-structured environmental (*sp-en*), and purely spatial (*sp*) variables
287 on species distributions (Borcard et al. 1992). Canonical ordinations are biased by the number of
288 predictor variables and sample size (Peres-Neto et al. 2006), so we employed the estimators of
289 Peres-Neto et al. (2006) to control for this bias and to test the significance of the variance
290 fractions, as well as to test for significant differences between fractions.

291

292 ## Results

293 Fifteen taxa were identified from the lakes and ponds on northern Ellesmere Island

294 (Table 2). The most frequently found microcrustacean taxa were *Daphnia*
295 *middendorffiana/tenebrosa*, *Cyclops scutifer* and Chydoridae. Species found in this study that
296 had not previously been noted on Ellesmere Island included *Daphnia umbra* (Taylor et al. 1996),
297 *Artemiopsis stefanssonii* Johansen, and *Tachidius discipes* Giesbrecht. The frequency of
298 occurrence for the various taxa ranged from 2% to 80% of lakes on Ellesmere, with *D.*
299 *middendorffiana/tenebrosa* being the most common taxa. In general, most taxa occurred in a low
300 number of lakes; however, taxa in the warmer Lake Hazen region tended to occur with greater
301 frequency (Table 2).

302 Species richness varied from 0 to 9 taxa per lake, averaging 3.4 taxa per lake (Fig. 3).
303 Species richness in the Lake Hazen area was significantly greater than lakes in the rest of
304 northern Ellesmere Island (t = -4.73, $p < 0.01$, df = 52). Principal component 1 (PC1) explained
305 the majority of variation in species richness, with a small contribution from PC3 (Table 3). PC1
306 had high positive loadings with temperature, conductivity, calcium, DOC, TN, and TP, and
307 negative loadings with surface area, while PC3 had a high negative loading with elevation (Table
308 3). Species diversity, measured by the Shannon-Wiener index, was generally low in most lakes
309 and positively skewed by a large number of small values (mean: 0.45, median: 0.36) (Fig. 3).
310 Diversity was significantly greater in the Lake Hazen area than in northern Ellesmere (t = -2.77,
311 $p < 0.01$, df = 52). Evenness (mean: 0.46, median: 0.41) (Fig. 3) was significantly greater in
312 northern Ellesmere than in the Lake Hazen region (t = 2.38, p = 0.01, df = 52).

313 The overall RDA of all the Ellesmere Island sampling sites was significant (trace = 0.39,
314 F = 4.82, $p < 0.01$) and we found the first axis was driven by productivity (TP), ice cover, and
315 broad-scale spatial variation (**broad2**), differentiating between sites in the Lake Hazen region
316 and sites on the rest of the island (λ_1 = 0.28, F = 18.15, $p < 0.01$) (Fig. 4). *Daphnia.*

317 *middendorffiana/tenebrosa* and *Brachinecta paludosa,* an anostracan, were positively associated
318 with TP, while juvenile stage copepods were positively related to ice cover. The second axis (λ_2
319 = 0.04) was structured by elevation (likely a proxy for temperature and/or isolation) and different
320 meso-scale (**meso3, meso5**) spatial variables. Cyclopoid and harpacticoid copepods, bosminids,
321 and chydorids were positively associated with elevation, and were associated with meso-scale
322 spatial variables **meso3 and meso5**.

323 The Lake Hazen area RDA was also significant (trace = 0.58, $F = 3.84$, $p < 0.01$);
324 however, its first axis was controlled by DOC and elevation (Fig. 5). The variables TN and TP
325 were highly correlated with DOC, and were therefore removed as active variables in the analysis.
326 DOC was positively associated with *D. middendorffiana/tenebrosa* and adult *B. paludosa*, while
327 elevation was positively correlated with juvenile copepods and juvenile and adult anostracans
328 ($\lambda_1 = 0.34$, $F = 8.91$, $p < 0.01$). The second axis ($\lambda_2 = 0.11$) was driven by spatial variables. Broad
329 regional-scale variables **very broad2** and **very broad3,** as well as meso-scale variable **meso2,**
330 were positively associated with several cyclopoid and harpacticoid copepod taxa, bosminids,
331 chydorids, and juvenile notostracans. *Holopedium gibberum* and ostracods were positively
332 correlated with meso-scale variable **meso1**. The supplementary environmental variables TN and
333 TP were highly positively correlated with DOC in both the Lake Hazen area and all of
334 Ellesmere, suggesting that DOC and nutrients are likely the most important variables in lakes on
335 Ellesmere Island.

336 Species that are thought to be effective dispersers, such as the fairy shrimp, *Brachinecta*
337 *paludosa* (Bohonak and Whiteman 1999), and the pigmented *D. middendorffiana/tenebrosa*
338 (Mellors 1975), were highly correlated with broad spatial scales at the Lake Hazen region (Table
339 4). As an example, *D. middendorffiana/tenebrosa* was positively associated with the white

sampling locations generated by broad-scale spatial variable **broad2** (Fig. 2b). In addition, *D. middendorffiana/tenebrosa* was also highly correlated with very broad and broad spatial variables at the larger Ellesmere Island scale. In addition, most cladoceran taxa, juvenile notostracans, ostracods, and nauplii were correlated with very broad and broad spatial structures, suggesting that they have broad distributions. Several cyclopoid and harpacticoid copepod taxa were also highly correlated with very broad and broad spatial scales in both ordinations.

Variation in microcrustacean communities in the Lake Hazen area was mostly explained by purely environmental (*en)* and purely spatial (*sp)* variables, which contributed 29 and 21% of variation, respectively (Fig. 6). In contrast, purely spatial variables contributed very little to overall variation in microcrustacean composition at the larger Ellesmere Island scale (7%), while purely environmental variables explained a similar amount of variation at both scales (Ellesmere: 23%, Lake Hazen: 29%) (Fig. 6). Spatially-structured environmental (*sp-en)* variables explained little variation at both scales (< 4%). Pure spatial and pure environmental variation were significantly different from zero in the Lake Hazen and Ellesmere Island datasets (all variables: $p < 0.01$). As well, there was no difference between environmental and spatial variation at the Lake Hazen scale ($p = 0.60$), but environmental variables explained more variation than spatial variables in Ellesmere Island communities ($p = 0.04$).

Discussion

Our survey of lakes and ponds on northern Ellesmere Island revealed patterns of species richness and composition that are consistent with climate-induced environmental gradients and spatial structuring. Microcrustacean richness and distribution were correlated with variables that can be influenced by a warmer climate, such as greater nutrient and DOC concentrations

363 resulting from increased terrestrial vegetation, and greater conductivity as a result of evaporative
364 concentration of solutes (Keatley et al. 2007). Additionally, microcrustaceans were structured by
365 variables associated with dispersal-limitation, such as elevation. While some of the common
366 relationships between environmental variables and microcrustaceans that have been observed in
367 temperate systems were also observed in our study, we found that other variables, such as DOC,
368 can influence Arctic microcrustacean communities. We found evidence of spatial patterns,
369 especially around Lake Hazen, where 21% of variation in species distributions was due to the
370 structuring of communities by spatially-related factors, which probably results from dispersal
371 between nearby lakes. However, we also observed low frequencies of microcrustacean taxa and
372 high beta diversity (Lande 1996), both at the Lake Hazen scale (59%) and for all the sites on
373 Ellesmere (73%), suggesting that dispersal is limiting in the harsh landscape of the Arctic.
374 The main determinants of species richness and composition in our study were nutrients,
375 conductivity (which was highly correlated with calcium), and DOC. While lake productivity
376 (Dodson et al. 2000; Jeppesen et al. 2000) and calcium (Wærvågen et al. 2002) are well-known
377 predictors of microcrustacean species richness and composition in temperate zones, DOC is
378 rarely a significant driver of microcrustacean community structure (Keller and Pitblado 1984;
379 Hessen et al. 2006) (but see Wissel et al. 2003). However, Olson et al. (1995) also found that
380 DOC and colour were important predictors of zooplankton community composition in a
381 chronosequence of lakes in Alaska, where increasing colour in older lakes altered competitive
382 and predator-prey interactions. In Arctic lakes, DOC primarily results from allochthonous input
383 from the surrounding watershed (Hamilton et al. 2001) and the humic content acts to reduce
384 microcrustacean mortality due to UV radiation (Rautio and Korhola 2002a). In the Lake Hazen
385 region, lakes have elevated concentrations of DOC and nutrients, probably resulting from the

386 lush vegetation associated with warmer temperatures in the polar oasis (Keatley et al. 2007);
387 however, lakes outside of this polar oasis had significantly lower DOC concentrations (t = -4.92,
388 $p < 0.01$, df = 26). In shallow study lakes, we would expect that increased melanization would be
389 the primary way that microcrustaceans, such as *Daphnia middendorffiana/tenebrosa*, would
390 avoid UV damage in low DOC lakes (Rautio and Korhola 2002b). However, we also expect *D.*
391 *middendorffiana/tenebrosa* to do well in high DOC lakes, where they would not produce as
392 much melanin (Rautio and Korhola 2002b), and this energy could therefore be redirected
393 towards growth and reproduction, increasing their competitive ability (Hessen 1996). In addition,
394 DOC from terrestrial sources can serve as a food source for microcrustaceans (Carpenter et al.
395 2005). Indeed, we observed a wide range of *D. middendorffiana/tenebrosa* relative abundances
396 at low DOC (<1-100% of adults at DOC $\leq$ 5 mg·L^{-1}; mean = 46%), but higher relative
397 abundances at high DOC (mean = 72%). The role of DOC in structuring microcrustacean
398 communities is likely related to mechanisms of UV avoidance and possibly also food
399 availability, and would likely be important in other systems where UV light penetration is high,
400 ie. high elevation and boreal lakes and ponds. The success of *D. middendorffiana/tenebrosa* may
401 also be due to a lack of fish predation, releasing it from the tradeoffs associated with its larger
402 size and pigmentation. Although we do not have fish data available for our study lakes, many of
403 the ponds probably freeze solid during the winter and would, therefore, not support fish
404 populations.

405 Temperature, temperature-related variables, e.g., surface area, and elevation were
406 secondary determinants of microcrustacean composition and richness. Lakes with large surface
407 areas tend to be colder and take longer to heat than small lakes, thus there is an inverse
408 relationship between temperature and surface area. Elevation is likely a proxy of both

409 temperature and isolation, as its negative influence on species richness and positive relationship
410 with juvenile stages probably reflects fewer microcrustacean propagules from upstream sources,
411 colder water temperatures, later ice-off dates, and thus, slower reproduction and development.
412 Hessen et al. (2006) found that high elevation lakes generally had low species richness, which
413 they attributed to difficulties in colonization. In contrast to the positive relationship that is
414 generally observed between surface area and microcrustacean richness in temperate lakes
415 (Dodson 1992), we found a negative relationship between surface area and microcrustacean
416 richness. Hessen et al. (2006) and Walseng et al. (2006) also failed to observe a positive
417 relationship between area and crustacean species richness at high latitudes. As larger lakes hold
418 more volume and take longer to heat, this suggests that temperature can override the positive
419 effect of area on microcrustacean richness. We acknowledge that as a result of sampling near the
420 shore, we may have missed some hypolimnetic taxa in larger lakes, which would be reflected by
421 lower species richness in larger lakes. However, the hypolimnetic *Cyclops scutifer* was detected
422 in almost 50% of lakes, including several of the largest lakes (Supplementary Tables S1 and S2),
423 suggesting that our sampling was representative of the microcrustacean community in lakes on
424 northern Ellesmere Island. Thus, high latitude microcrustacean communities appear to be
425 structured by different processes than temperate lake microcrustaceans, as in general, most
426 environmental predictors showed significant variability (Table 1), suggesting that our results are
427 not an artefact of sampling a restricted range of environmental conditions.

428 With temperatures in the Arctic expected to rise by 3-5°C by the end of the 21st century
429 (ACIA 2005), consideration of the effect of warming on microcrustaceans in these lakes is of
430 great importance. Temperature provides both direct, e.g., metabolic, and indirect, e.g. food
431 availability, mechanisms for change in microcrustacean communities. This tradeoff between

higher production and increased metabolic demands will likely favour smaller species (Moore et al. 1996). This was observed experimentally, where daphniid and overall zooplankton biomass declined in high elevation experimental ponds when the temperature was raised, likely responding to temperature-induced changes in algal composition (Strecker et al. 2004). Although we observed some small-bodied microcrustaceans (e.g., chydorids) in warmer locations, in general, the large-bodied *Daphnia* dominated assemblages in lakes with higher temperatures, such as those found in the polar oasis Lake Hazen region (15.3°C±4.9 in Lake Hazen sites vs. 8.5°C±4.7 in northern Ellesmere Island sites). This suggests that perhaps the thermal optimum of *Daphnia* has not yet been reached, but with increasing temperature, it will likely be vulnerable to higher metabolic costs.

Temperature also affects reproduction: directly, via accelerated development (Moore et al. 1996) and indirectly, by increasing the length of the growing season. Hebert and Hann (1986) suggested that calanoids are limited in the Arctic by the inability to shorten their life cycle and reproduce within the short growing season. We detected few adult calanoids, and the copepodids tended to be associated with larger lakes (Fig. 4a), probably because they do not freeze to the bottom and can maintain populations throughout the winter. Thus, a change in the length of the growing season may improve the establishment success and persistence of calanoids and other slow-developing taxa in small Arctic lakes.

Overall, the lakes on Ellesmere Island show low species richness, diversity, and frequency of occurrence in lakes. Although the species pool around Lake Hazen and northern Ellesmere Island is similar, average species richness was greater around Lake Hazen. The low frequency of occurrence of species suggests that dispersal limitation is a key factor in structuring these microcrustacean communities. This was also supported by the low fraction of variation

455 explained by spatial variables (7%) in the entire sample set on Ellesmere Island. Dispersal is
456 more likely to be limiting in regions where there are large physical barriers to the movement of
457 microcrustaceans and their vectors. Hessen et al. (2006) found evidence of dispersal limitation to
458 isolated mountainous lakes in a 300+ lake survey in Norway, a landscape similar to that of the
459 Arctic. In temperate systems, there is evidence of dispersal limitation when considering large
460 geographic regions (Shurin et al. 2000); however, at small geographic and experimental scales,
461 studies have found that dispersal is not limiting (Cottenie et al. 2003; Forrest and Arnott 2006).
462 Using variation partitioning, we observed large contributions of spatial and
463 environmental variables to patterns in microcrustacean composition, especially in the Lake
464 Hazen region. This is perhaps not surprising, as lakes in close proximity to each other would be
465 more likely to influence species distributions via increased opportunity for short-distance
466 dispersal events. Whiteside et al. (1980) found that recently-formed moraine ponds in the Yukon
467 had both calanoid and cyclopoid copepod species, as well as several cladoceran taxa, suggesting
468 that a number of high latitude species can disperse quickly into new locales, in contrast to the
469 view that passive dispersal in invertebrates is extremely limited (Bohonak and Jenkins 2003).
470 Factors explaining microcrustacean community variation at different spatial scales and in
471 different regions are generally consistent: spatial and environmental variables describe roughly
472 equal fractions of variation, with the exception of the two larger scale studies (Québec and
473 Ellesmere; Fig. 6), where dispersal is more likely to be limiting at large spatial scales where
474 long-distance dispersal events would be rare. Interestingly, fine-scale spatial variables were not
475 important explanatory variables at either the small Lake Hazen region or the larger Ellesmere
476 Island scale. This suggests that lakes that are very close together generally have similar
477 communities, in agreement with the review of Havel and Shurin (2004), who suggested that

dispersal could be rapid at distances <10 km, highlighting the importance of short distance frequent dispersal events. However, this may be species-specific: Hebert and Hann (1986) suggest that low dispersal rates have restricted the distribution of certain microcrustacean species, while Sarnelle and Knapp (2004) observed relatively rapid recolonization of lakes by *Daphnia middendorffiana* following removal of fish, but failed to detect the copepod *Hesperodiaptomus shoshone,* which they attributed to significant Allee effects.

In contrast, broad and very broad-scale spatial variables were important at both the Lake Hazen and Ellesmere Island scale, suggesting that there are likely some large barriers to dispersal that impede species from broadly colonizing the island. In the case of Ellesmere Island, the continuing retreat of the glaciers means that younger lakes, found closer to the glaciers, may show community compositions that exclude some of the slower dispersing species. In addition, younger lakes tend to have lower DOC concentrations and higher UV penetration, which will likely also affect species establishment and composition (Williamson et al. 2001). Finally, although we detected significant contributions of spatial and environmental variables to the total variation explained in microcrustacean community composition, a large portion of variation remained unexplained (Fig. 6). This likely reflects our one-time sampling, which may have failed to capture important variation in environmental variables, as well as the entire microcrustacean community, which can be underestimated by 50% by single sampling visits (Arnott et al. 1998).

Local biotic factors are also an important determinant of microcrustacean species composition. We used nutrients as a proxy for phytoplankton productivity, as they represented a better measure of productivity than chl *a*, which has been shown to be poorly correlated with nutrients in Arctic lakes and ponds, where the predominant contributor is periphytic production (Keatley et al. 2007). Although the lakes in this study are generally fishless, there are other

predators that may have an influence on the composition of microcrustaceans. Larger omnivorous copepods may have preyed on small-bodied microcrustaceans; however, these large predators were relatively rare in our study, as most assemblages were dominated by *D. middendorffiana/tenebrosa* or juvenile herbivorous stages of copepods. Other predator groups, such as waterbirds and larval insects, could also have influenced our results. For example, the migratory Red Phalarope waterbird (*Phalaropus fulicarius* (Linnaeus)), can consume *Daphnia*; however, predation rates are low at natural bird densities, suggesting that their impact is minimal (Dodson and Egger 1980). In addition, dipteran larvae were often found in microcrustacean samples, but their abundance was generally low.

Our survey revealed several species that had not been previously detected in lakes on Ellesmere Island. *Artemiopsis stefanssoni*, an anostracan, was identified on Ellesmere Island for the first time in this study. However, it is common throughout the Arctic, including northern Canada and eastern Greenland, and thus, Røen (1981) speculated that *A. stefanssoni* was present on Ellesmere in 1965, but that it was missed in his sampling. *Daphnia umbra* was first identified as a distinct species within the *D. longispina* complex by Taylor and Hebert (1994) and named by Taylor et al. (1996). Although there are records for this species in the lower Arctic, until now there were no records for *D. umbra* or *D. longispina* on Ellesmere Island. Similarly, *Tachidius discipes* has been recorded from other sites in the Arctic (Tash 1971), but not previously from Ellesmere Island. As a result of the scarcity of studies in this area, it is difficult to assess whether these species have recently dispersed to Ellesmere Island or whether these species were simply not detected in previous studies. Experimental evidence has found that warming can reduce the invasion resistance of natural zooplankton communities (Holzapfel and Vinebrooke 2005), suggesting that a changing climate may facilitate species colonizations into new habitats. We

hope that our study will provide important baseline information about microcrustacean communities against which future changes can be assessed.

Our study has found that the major controls on microcrustacean richness and community composition are factors that are closely related to climate. The Arctic is expected to be subjected to increased temperatures and precipitation in the coming decades (ACIA 2005). Warmer temperatures have altered both the biotic and abiotic characteristics of Arctic lakes. Decreased ice cover has led to longer growing seasons, which have been linked to greater productivity (Smol and Cumming 2000). Nutrients, DOC, and temperature were limiting factors in microcrustacean species distributions in our study, and the release of these constraints with increased warming could allow increased numbers of more southern species to colonize Ellesmere Island. Additionally, we demonstrated that High Arctic microcrustacean communities are structured differently than communities at lower latitudes: dispersal limits the ability of microcrustaceans to broadly colonize lakes and ponds on Ellesmere Island, while strong environmental gradients linked to climate change, i.e., high concentrations of DOC and nutrients flushed in from the watershed, are important determinants of survival and long-term persistence in the region.

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746

747 Table 1. Median, range, and standard deviation of physical, chemical, and biological
748 characteristics of all study lakes. Abbreviations: chl *a* = chlorophyll *a*, TP = total phosphorus,
749 TN = total nitrogen, DOC = dissolved organic carbon.

	Median	Range	Standard deviation
Elevation (m)	221	1 - 1006	244
Surface area (ha)	1.5	0.01 - 54200	7370.9
Surface temp (ºC)	12.5	0.5 - 22.0	5.7
Ice cover	0.0	0 - 1	0.4
pH	8.3	7.5 - 9.0	0.3
Conductivity ($\mu S \cdot cm^{-1}$)	174	30 - 1650	379
SiO_2 ($mg \cdot L^{-1}$)	1.64	0.13 - 13.90	3.40
Chlorine ($mg \cdot L^{-1}$)	1.46	0.12 - 32.4	7.43
Calcium ($mg \cdot L^{-1}$)	29.7	3.2 - 451	85.3
Chl *a* ($\mu g \cdot L^{-1}$)	0.50	0.1 - 1.6	0.42
TP ($\mu g \cdot L^{-1}$)	3.6	1.0 - 10.5	2.5
TN ($mg \cdot L^{-1}$)	0.33	0.06 - 1.99	0.56
DOC ($mg \cdot L^{-1}$)	4.5	0.6 - 40.1	11.0

750

751 Table 2. Proportion of lakes and ponds occupied by crustacean taxa found in the Lake Hazen
752 area and northern Ellesmere Island.

Taxonomic affiliation	Abbreviation	Lake Hazen area, Ellesmere Island	Northern Ellesmere Island
Subphylum Crustacea			
Class Branchiopoda			
Order Anostraca			
Branchinecta paludosa (Müller)	*B.palud*	0.63	0.20
Artemiopsis stefanssoni Johansen	*A.stefan*	0.04	0.07
Juvenile Anostraca	juv Anostr	0.21	0.07
Order Cladocera			
Daphnia middendorffiana/tenebrosa (see text)	*D.mid/ten.*	1.00	0.60
Daphnia umbra Taylor et al. (1996)	*D.umbra*	--	0.03
Bosmina freyi/liederi DeMelo and Hebert (1994)	*B.fr/li*	0.13	0.13
Chydoridae	Chydorid	0.75	0.27
Holopedium gibberum Zaddach	*H.gibber*	0.04	--
Order Notostraca			
Lepidurus arcticus (Pallas)	*L.arct*	0.04	0.03
Juvenile Notostraca	juv Notostr	0.21	--
Class Maxillopoda			
Subclass Copepoda			
Order Calanoida			
Limnocalanus macrurus Sars	*L.macru*	--	0.03
Calanoid copepodid	cala cpd	0.08	0.23
Nauplii	nauplii	0.83	0.77
Order Cyclopoida			
Eucyclops agilis (Koch)	*E.agilis*	0.67	0.10
Megacyclops magnus (Marsh)	*M.magnus*	0.46	0.03
Cyclops scutifer Sars	*C.scutifer*	0.33	0.57
Cyclopoid copepodid	cycl cpd	0.96	0.63
Order Harpacticoida			
Tachidius discipes Giesbrecht	*T.discip*	--	0.03
Attheyella nordenskioldii (Lilljeborg)	*A.norden*	0.21	0.07
Harpacticoid copepodid	harp cpd	0.29	0.17
Class Ostracoda	Ostracod	0.46	0.17

753
754

755 Table 3. (a) Multiple regression of principal component variables to predict species richness.
756 Smaller values of Mallows C_p and AIC indicate the most parsimonious model. AIC= Akaike's
757 information criterion. (b) Loading of environmental variables on principal components axes.
758 Values in bold indicate variables with high loadings (>0.7), while italicized variables indicate
759 moderately high loading. Abbreviations: chl *a* = chlorophyll *a*, DOC = dissolved organic carbon,
760 TN = total nitrogen, TP = total phosphorus.

(a)	Adj R^2	C_p	AIC	*F*-ratio	*p*-value	Variable	Coefficient	Partial correlation coefficient	*t*-value	*p*-value
Model 1	0.39	1.28	59.55	18.23	<0.01*	PC1	0.62	0.63	5.84	<0.01*
						PC3	-0.16	-0.21	-1.53	0.13
Model 2	0.38	1.52	57.96	33.27	<0.01*	PC1	0.62	0.62	5.77	<0.01*

(b)	PC1	PC2	PC3	PC4
latitude	-0.3104	**-0.7551**	0.2853	-0.4111
temperature	**0.8458**	0.0630	0.1103	0.0717
conductivity	**0.8773**	0.2919	0.2069	0.0448
calcium	**0.8379**	0.3512	0.1811	0.0890
chl *a*	0.1707	**-0.7260**	0.0127	0.5826
DOC	**0.9297**	-0.1951	-0.0617	-0.1868
TN	**0.8540**	-0.1626	-0.1553	-0.3642
TP	**0.9018**	-0.2657	-0.0323	-0.1777
elevation	0.0596	-0.0281	**-0.9742**	-0.0368
surface area	*-0.6837*	0.2232	0.0921	-0.3592

761 * $p < 0.05$
762

763 Table 4. Species scores on canonical axis 1 for individual spatial submodels. Values in **bold**
764 indicate species with high loadings (>0.3), while *italicized* variables indicate moderately high
765 loading (0.2-0.3). Only significant spatial submodels are presented. Species abbreviations as in
766 Table 2.

	Lake Hazen	Ellesmere	
spatial scale	broad	very broad	broad
spatial variables	**broad4-5**	**very broad1-2**	**broad3-11**
B.palud	**-0.4856**	0.1828	-0.0555
A.stefan	**0.3758**	0.0662	0.0791
Juv Anostr	**0.5675**	0.0277	-0.0435
D.mid/ten	**-0.6034**	**0.3698**	**-0.5764**
D.umbra		-0.1306	*0.2609*
B.fr/li	*0.2266*	0.0838	*0.2573*
Chydorid	**-0.3283**	*0.2734*	-0.0873
H.gibber	-0.0804	0.0534	*-0.2800*
L.arct	-0.1695	0.1023	-0.1379
Juv Notostr	*0.2049*	**0.4294**	**0.3098**
L.macru		-0.0196	0.0669
Cala cpd	*-0.2303*	-0.0487	0.1205
Nauplii	**0.5117**	*-0.2887*	**0.4337**
C.scutifer	**0.3115**	-0.1738	*0.2772*
E.agilis	-0.0199	**0.6001**	0.1106
M.magnus	-0.1089	**0.4795**	-0.0152
Cycl cpd	**0.4081**	-0.1202	0.0074
A.norden	0.1697	*0.2070*	0.1446
T.discip		-0.0935	0.0667
Harp cpd	0.0019	0.0499	*0.2233*
Ostracod	-0.1154	0.0835	*-0.2009*

767

768

769

Figure Captions

Figure 1. Study location in (a) northern Canada, with sampling sites on (b) northern Ellesmere Island and (c) the Lake Hazen area.

Figure 2. Examples of spatial eigenvectors of the Lake Hazen site at progressively finer scales. Circles are plotted at sampling locations, where larger circles represent larger positive (grey) or negative (white) values of the eigenvector. (a) Variable **very broad1**, representing the largest regional-scale variability, (b) variable **broad2**, representing broad-scale variability, (c) variable **meso2**, representing intermediate- or meso-scale variability, and (d) variable **fine1**, representing fine local-scale variability. Notice that at the very broad scale, sites are grouped into two clusters, with increasing numbers of clusters at progressively finer scales.

Figure 3 (a) Richness, (b) Shannon-Wiener diversity, and (c) Simpson's evenness distributions in lakes on Ellesmere Island.

Figure 4. A redundancy analysis of microcrustacean communities from all sample sites on Ellesmere Island. (a) Species and (b) sample sites (● = Lake Hazen area, ○ = northern Ellesmere) in relation to environmental and spatial variables. Species are represented by thin vectors and are italicized (see Table 2 for abbreviations), environmental (see Table 1 for abbreviations) and spatial variables are represented by thick vectors and by boldface type, and supplementary environmental variables are shown with grey dashed-line vectors and bold-italic type. Spatial variables are abbreviated **broad2** (broad-scale variable 2), **meso3** (meso-scale variable 3), and **meso5** (meso-scale variable 5).

Figure 5. A redundancy analysis of microcrustacean communities from sites around Lake Hazen. (a) Species and (b) sample sites in relation to environmental and spatial variables. Species are represented by thin vectors and are italicized (see Table 2 for abbreviations), environmental

(see Table 1 for abbreviations) and spatial variables are represented by thick vectors and by boldface type, and supplementary environmental variables are shown with grey dashed-line vectors and bold-italic type. Spatial variables are abbreviated **very broad2** (very broad-scale variable 2), **very broad3** (very broad-scale variable 3), **meso1** (meso-scale variable 1), and **meso2** (meso-scale variable 2).

Figure 6. Comparison of variation explained in microcrustacean communities in Cottenie et al. (2003), Beisner et al. (2006), Pinel-Alloul et al. (1995), Lake Hazen, and Ellesmere Island. Variation in species abundances is explained by purely environmental (*en*: black bars), spatially-structured environmental (*sp-en*: hatched bars), and purely spatial (*sp*: grey bars) variables, where the remaining variation is unexplained by the examined variables (white bars). Study area listed on right side of graph.

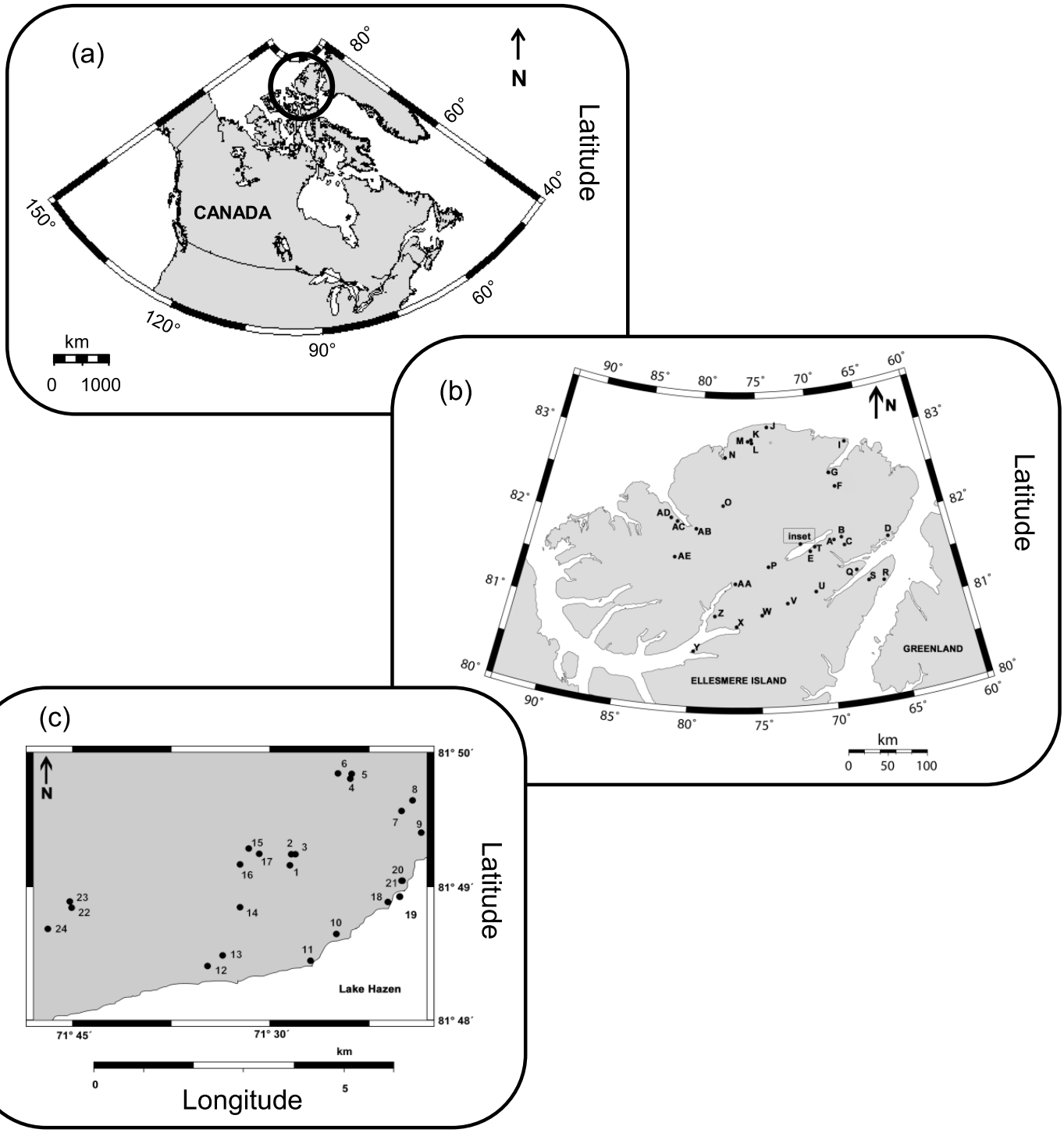
(a)
N
80°
60°
40°
150°
120°
90°
60°
CANADA
km
0 1000
Latitude
(b)
90° 85° 80° 75° 70° 65° 60°
83°
82°
81°
80°
N
AD
AC
AB
AE
AA
inset
A
B
C
D
E
T
P
Q
S
R
U
V
W
Z
X
Y
GREENLAND
ELLESMERE ISLAND
km
0 50 100
Latitude
(c)
N
81° 50´
81° 49´
81° 48´
71° 45´
71° 30´
Lake Hazen
km
0 5
Longitude
Latitude

Fig. 1

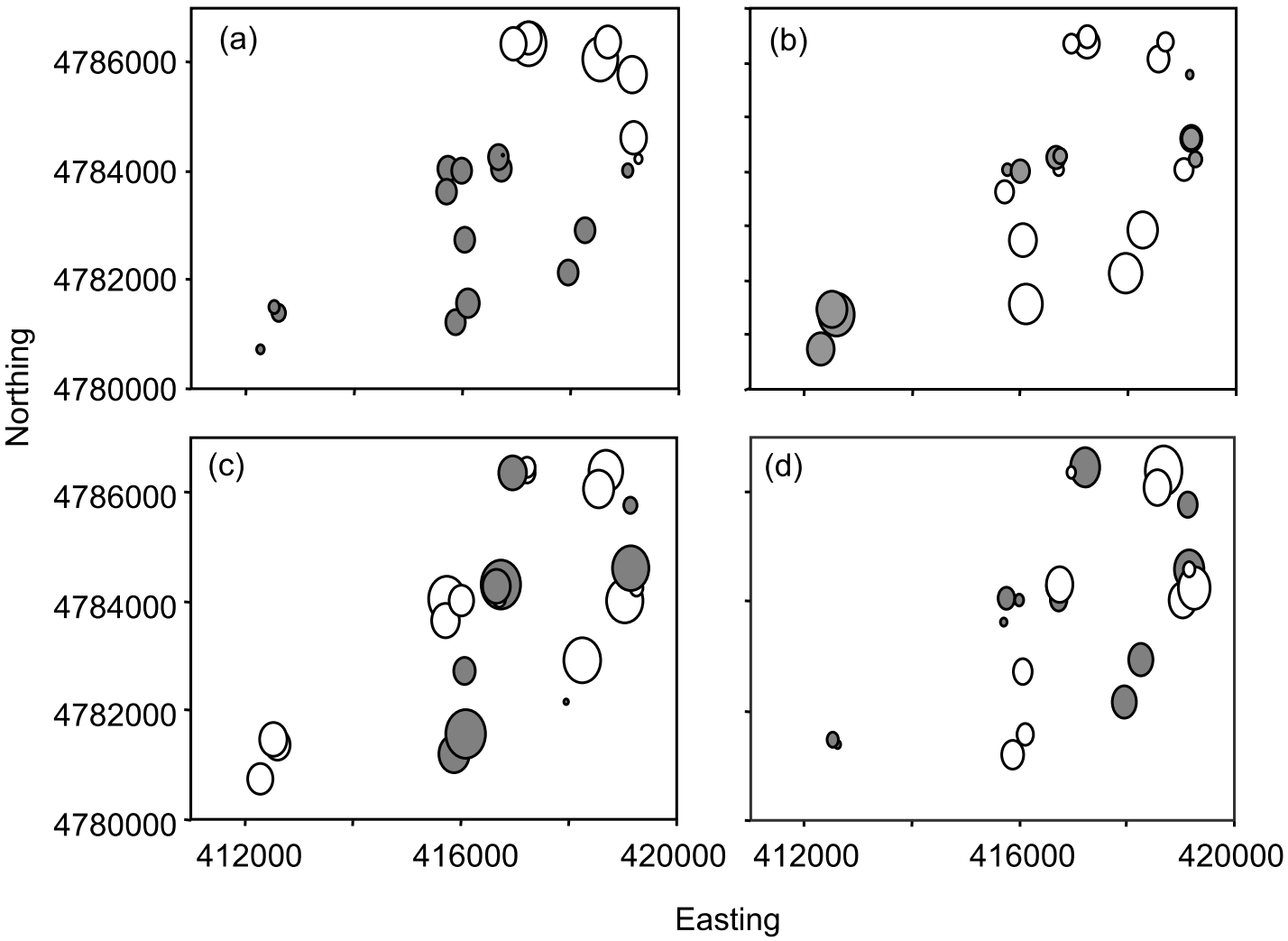
(a)
(b)
(c)
(d)
4786000
4784000
4782000
4780000
Northing
412000
416000
420000
Easting

Fig. 2

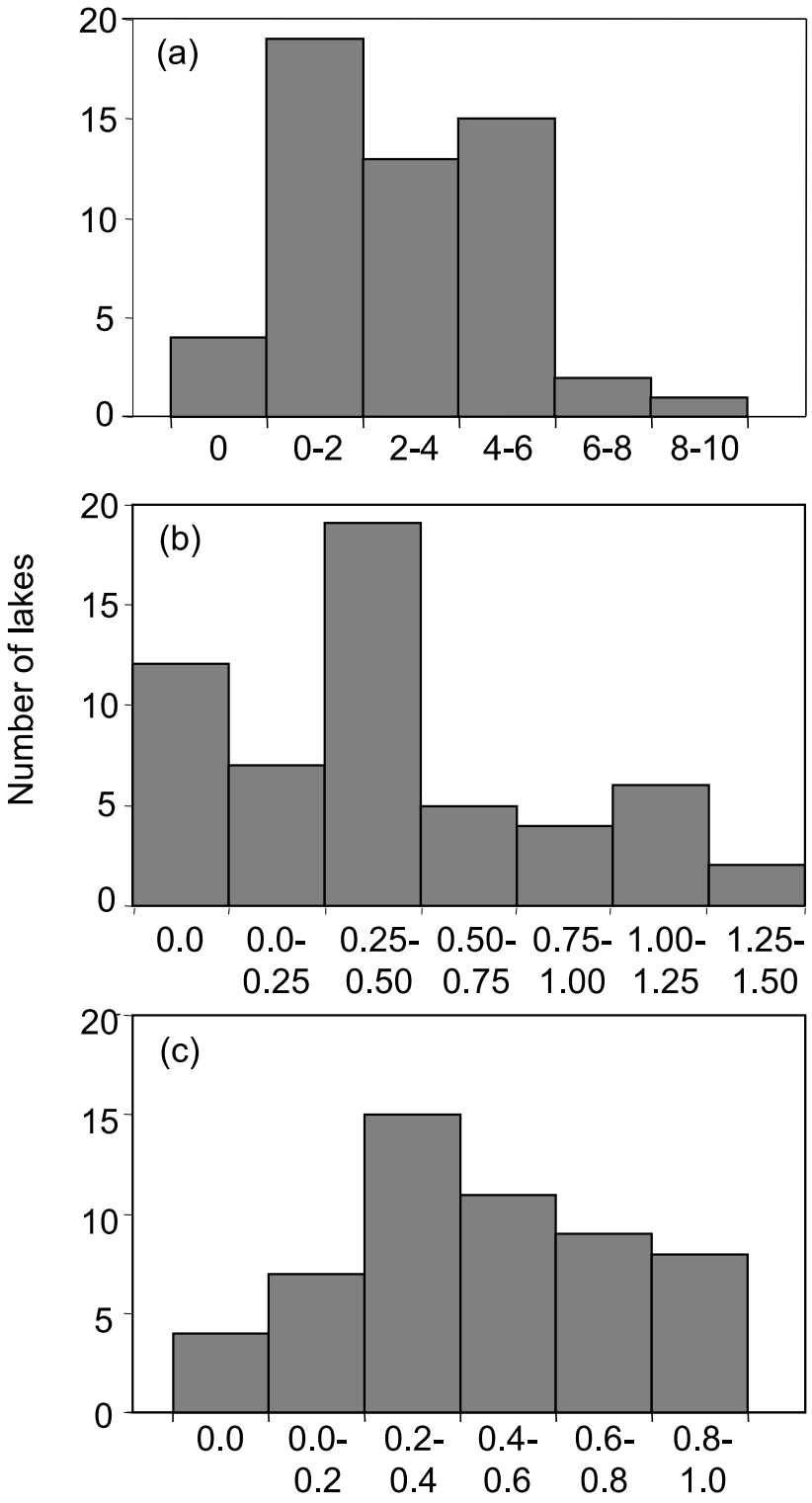
(a)
20
15
10
5
0
0
0-2
2-4
4-6
6-8
8-10
(b)
Number of lakes
0.0
0.0-0.25
0.25-0.50
0.50-0.75
0.75-1.00
1.00-1.25
1.25-1.50
(c)
0.0
0.0-0.2
0.2-0.4
0.4-0.6
0.6-0.8
0.8-1.0

Fig. 3

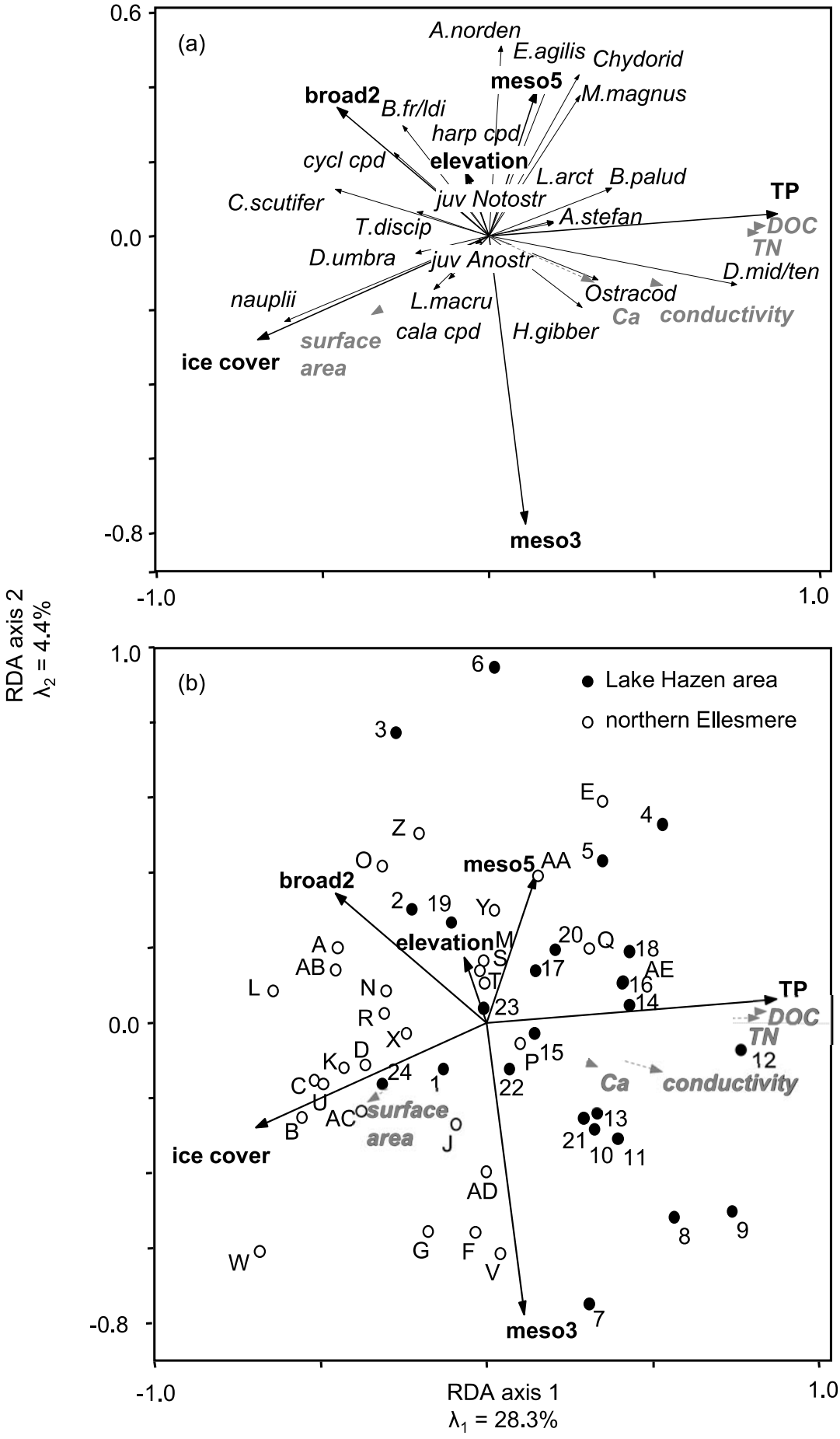
(a)
A.norden
E.agilis
Chydorid
meso5
M.magnus
broad2
B.fr/ldi
harp cpd
cycl cpd
elevation
L.arct
B.palud
C.scutifer
juv Notostr
TP
T.discip
A.stefan
DOC
TN
D.umbra
juv Anostr
D.mid/ten
nauplii
L.macru
Ostracod
Ca
conductivity
surface area
cala cpd
H.gibber
ice cover
meso3
0.6
0.0
-0.8
-1.0
1.0
RDA axis 2
λ2 = 4.4%
(b)
Lake Hazen area
northern Ellesmere
meso5
broad2
elevation
TP
DOC
TN
Ca
conductivity
surface area
ice cover
meso3
1.0
0.0
-0.8
-1.0
1.0
RDA axis 1
λ1 = 28.3%

Fig. 4

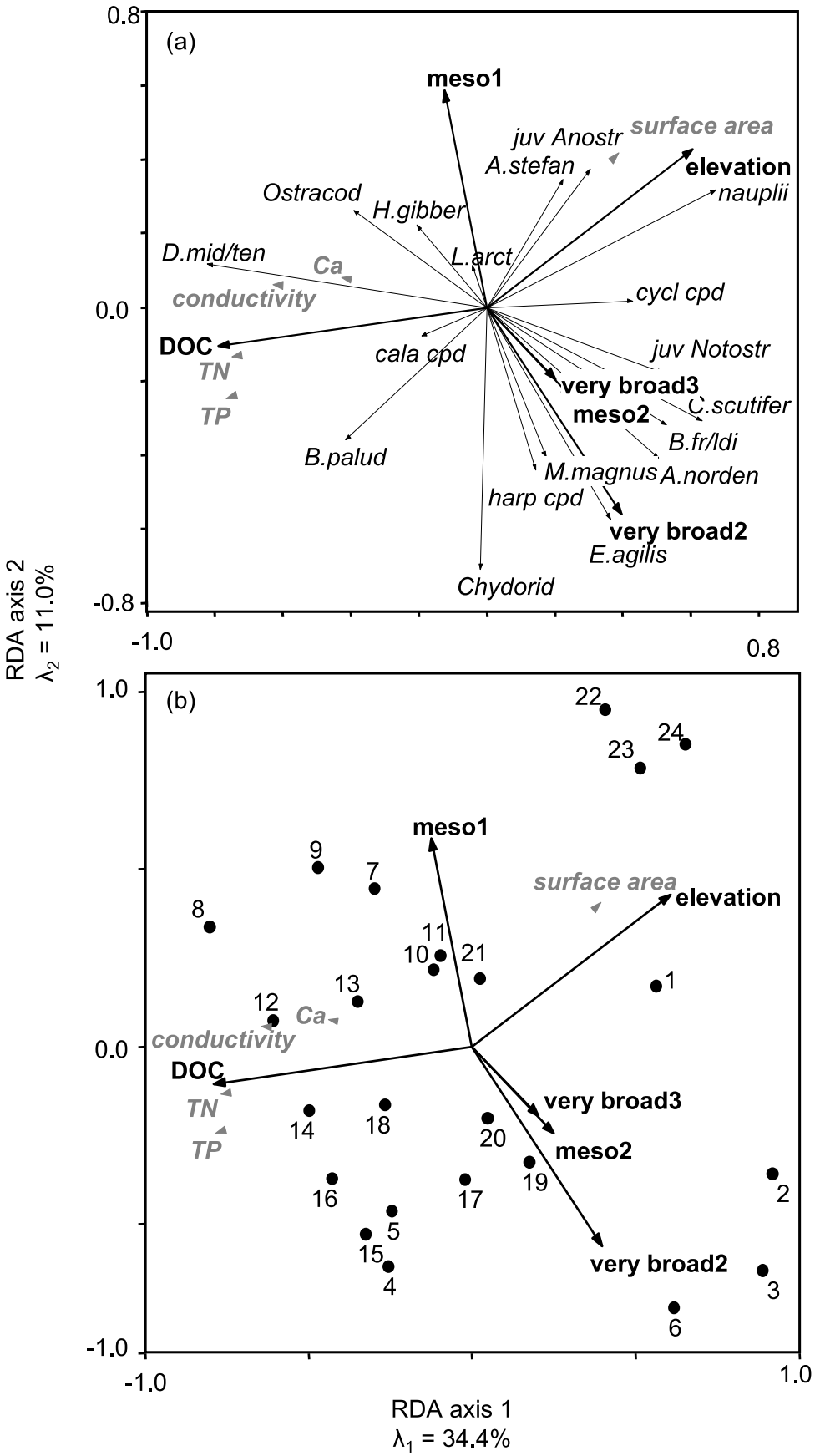
(a)
meso1
juv Anostr
surface area
A.stefan
elevation
Ostracod
H.gibber
nauplii
D.mid/ten
Ca
L.arct
conductivity
cycl cpd
DOC
cala cpd
juv Notostr
TN
very broad3
TP
meso2
C.scutifer
B.palud
B.fr/ldi
M.magnus
A.norden
harp cpd
very broad2
E.agilis
Chydorid
0.8
0.0
-0.8
-1.0
0.8
RDA axis 2
λ2 = 11.0%
(b)
22
24
23
meso1
9
7
surface area
elevation
8
11
10
21
1
13
12
Ca
conductivity
0.0
DOC
very broad3
TN
14
18
20
TP
meso2
19
2
16
17
5
15
very broad2
4
3
6
1.0
-1.0
-1.0
1.0
RDA axis 1
λ1 = 34.4%

Fig. 5

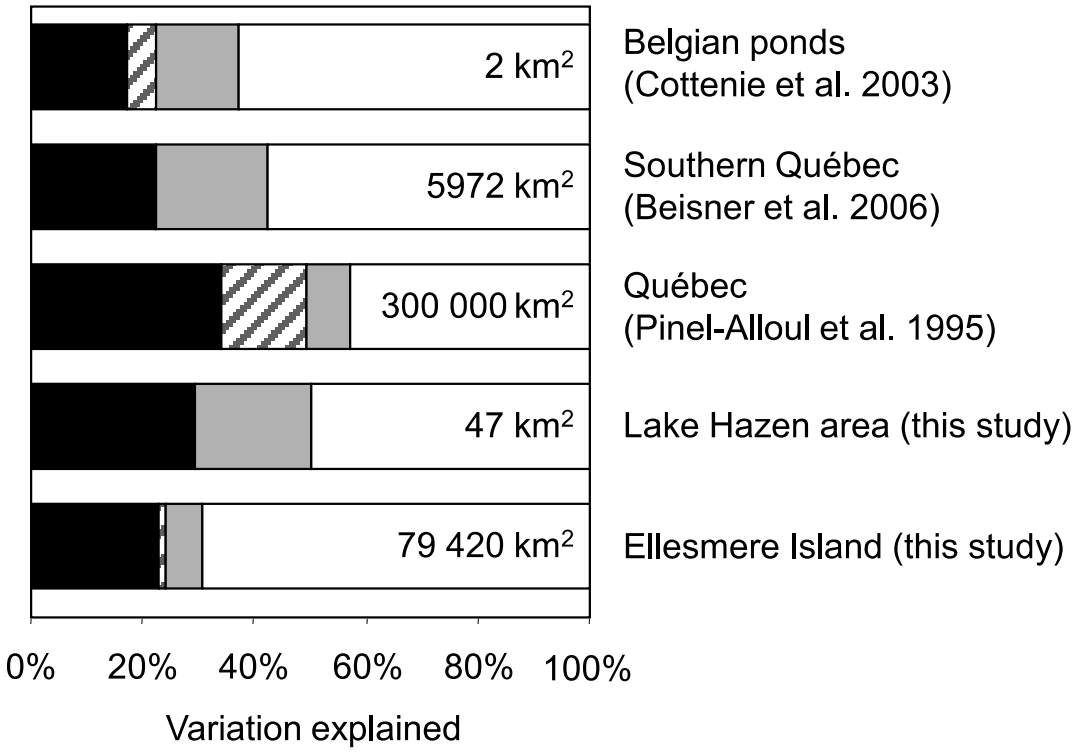
2 km²
5972 km²
300 000 km²
47 km²
79 420 km²
Belgian ponds
(Cottenie et al. 2003)
Southern Québec
(Beisner et al. 2006)
Québec
(Pinel-Alloul et al. 1995)
Lake Hazen area (this study)
Ellesmere Island (this study)
0%
20%
40%
60%
80%
100%
Variation explained

Fig. 6